Is Separating Resource Competition from Allelopathy Realistic?

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I. Abstract

Allelopathy and resource competition have often been suggested to explain plant–plant interference. Many studies have attempted to separate these two mechanisms of interference to demonstrate either as a probable cause of an observed growth pattern. We, however, are of the opinion that separating allelopathy from resource competition is essentially impossible in natural systems. Furthermore, any experimental design to separate allelopathy and resource competition will create conditions that will never occur in nature. In this article, the ecological interaction between allelopathy and resource competition in natural systems is discussed.

II. Introduction

The two mechanisms generally proposed to explain plant interference are resource competition and allelopathy (Harper, 1977; Rice, 1984, 1995; Grace & Tilman, 1990). Nature, however, is very complex, and there are many factors interacting simultaneously and/or sequentially. It is certainly very difficult to separate resource competition and allelopathy in natural systems. Allelopathy can be defined as any direct or indirect effect (harmful and/or beneficial) by one plant (including microorganisms) on another through production of chemical compounds that escape into the environment (Rice, 1984). Demonstrating allelopathy involves not only isolating compounds but also demonstrating that a toxic effect on other plant species is primarily the function of a compound and that when other interactions such as resource limitations are alleviated, the allelopathic effect persists. There are situations where allelopathy has evolved in response to resource competition (Williamson, 1990). Thus, it is important to evaluate the relative contribution of each of the two mechanisms in most of the studies on plant interference. Furthermore, in many situations it may not be possible to identify allelopathic compounds because responses of bioassay species may be due to a complex combination of toxic and nontoxic organic compounds present in low concentrations (Blum, 1996). The objectives of this article are to discuss how factors such as shade, drought, and nutrient stress interact with competition and allelopathy; and to discuss how competition and allelopathy may interact in natural systems.

In weed–crop and weed–weed interactions, competition is due mainly to removal of light, water, and nutrients by neighboring plants (Aldrich, 1987; Zimdahl, 1993). Allelopathy results when plants release into the environment chemicals that usually inhibit the growth of another plant. Competition creates only adverse effects due to a paucity of resources for growth and establishment of crops (Zimdahl, 1993). Allelopathic interference includes inhibitory and promoting effects (Rice, 1986), but inhibitory effects are the focus of this note. How do these mechanisms interact in nature to bring about interference?

Oksanen (1993) discussed how undisturbed communities are structured by competition which depends on environmental conditions. For example, ericaceous shrubs are more competitive in nutrient-poor habitats; evergreens are supposed to be competitive in boreal forests. Grime (1977, 1979) argued that competitive ability is inversely related to stress tolerance. He believed that stress not only excludes competitive species but also reduces importance of competition as a force in the structuring of plant communities. However, there is evidence that stress may induce allelopathy as a force in such structuring (Einhellig, 1989) and enhance the production of allelopathic compounds (Chou, 1983; Einhellig, 1989; Putnam, 1985; Tang et al., 1995). While reviewing allelopathy in cropping systems, Einhellig (1996) stated, "Allelopathy is strongly coupled with other stresses of the crop environment, including insect and disease, temperature extremes, nutrients and moisture variables, radiations, and herbicides." Allelopathy is strongly influenced by habitat ecology and environmental factors (Inderjit et al., 1996; Inderjit, 1997). What is not clear is how stress reduces the importance of competition and makes allelopathy a major force in the structuring of plant communities. How do stresses such as shade, drought, and low nutrients accelerate competitive and allelopathic interference? While plants compete for resources under shade and drought and in nutrient-limited environments, these stress factors are also known to enhance the production of secondary metabolites. Many secondary metabolites such as phenolics and terpenoids are known to complex with inorganic ions and influence accumulation of soil nutrients. These aspects are outlined in Figure 1.
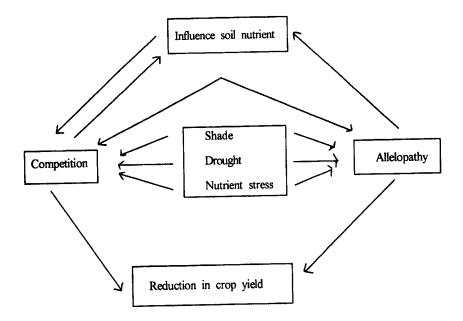
Fig. 1. Interaction of resource competition and allelopathy in a natural system.

III. Shade

Light is one of the important environmental factors for which weeds and crops may compete. During early stages of the crop life cycle, shade may not necessarily reduce crop yield, because crops can compensate for some early loss of total photosynthesizing area (Aldrich, 1987). However, shade may enhance the production of allelopathic compounds. Zucker (1963) reported that, compared to darkness, a short exposure of low-intensity light doubled the rate of chlorogenic acid synthesis. Bhowmik and Doll (1983) investigated the allelopathic effects of redroot pigweed (*Amaranthus retroflexus*) and yellow foxtail (*Setaria glauca*) residues on corn (*Zea mays*) and soybean (*Glycine max*) at different temperatures and photosynthetic photon flux densities (PPFD). They found that allelopathic effects of weed residues on corn were influenced by temperature and PPFDs. Tanrisever et al. (1987) isolated a dihydrochalcone ceratiolin from *Ceratiola ericoides* which, when exposed to light, decomposes to hydrocinnamic acid, which is highly inhibitory to grass growth. Moreover, there may also be modifications in the amount of allelopathic substances when two plants compete for light (Einhellig, 1989).

IV. Drought

Competition for water may account for significant crop yield reductions, but the competition for water during early stages of crop life cycle is unlikely (Aldrich, 1987). Drought can cause an increase in the amount of allelopathic compounds (Gershenzon, 1984). It has been shown that allelopathic activities are more pronounced when bioassay species grow under water stress (Einhellig, 1987, 1989). Many cyanogenic glycosides have been implicated in al-

lelopathy (Rice, 1984). Manifold increases in concentrations of cyanogenic glycoside have been reported in cassava (*Manihot esculenta*), grain sorghum (*Sorghum bicolor*), and sudangrass (*Sorghum sudanese*) (Nelson, 1953; Eck, 1976; Gershenzon, 1984). Majek et al. (1980) reported that the levels of cyanogenic glycosides increase with drought. Freeman and Mossadaghi (1971) reported that water-deficit conditions increase the level of isothiocyanates and other sulfur-containing secondary metabolites in *Rorippa nasturtium-aquaticum*. Various studies have reported increases in alkaloid concentrations with water stress in *Nicotiana rustica, N. tabacum, Datura innoxia, Hyoscyamus muticus, Solanum aviculare, Senecio longolobus*, and *Phalaris aquatica*, among others (Ball & Hoveland, 1978; Waller & Nowacki, 1978; Campbell & Seaborn, 1972; Gershenzon, 1984). However, these studies were not conducted to investigate the allelopathic activities of particular plant species.

Del Moral (1972) found that drought stress resulted in increased concentrations of chlorogenic and isochlorogenic acids. However, levels of cinnamic and benzoic acid derivatives in *Triticum aestivum* decreased under drought conditions (Tsai & Todd, 1972). Tevini et al. (1983) reported that water stress increased flavonoid content in cucumber cotyledon after 8 days of growth. Tang et al. (1995) found that marigold (*Tagetes erecta*) water-deficit transplanting and preblooming stages had higher free phenolic acids concentrations as compared to unstressed plants. Root exudates from rye (*Secale cereale*) inhibit root growth of wild oat (*Avena fatua*) (Tang et al., 1975). Richardson and Bacon (1993) identified the compounds as 2,4-dihydroxy-2H-1,4-benzoxazin-3-one (DIBOA) and its precursor, 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-one (DIMBOA), and demonstrated that their concentrations increased with drought stress.

Water stress could increase terpenoid level in the tissue, and qualitative variations in terpenoids have also been reported under drought conditions (Gershenzon, 1984). During dry periods of the year, the phenolic monoterpenes thymol and carvacrol were the main essential oils of *Thymus serrulatus*; however, during wet periods, an acyclic monoterpene, linalool, was the main essential oil (Hegnauer, 1966). Gilmore (1977) reported that water-deficit conditions increased the relative percentage of α-pinene in loblolly pine (*Pinus taeda*) and decreased the concentrations of β-pinene, camphene, myrcene, and limonene.

Dao (1987) demonstrated that with increased soil water content, the microbial population shifts toward facultative anaerobic organisms, which results in the degradation of allelopathic compounds through fermentation. At lower water potentials, oxygen could be limiting and result in a shift in the balance of the microbial population toward obligate anaerobic organisms (Dao 1987). Ardi (1986) found that the reduction of sweet corn (*Zea mays*) yield due to purple nutsedge (*Cyperus rotundus*) was most severe when the greatest water stress was imposed. Thus, growth inhibition of sweet corn may be due to the combined stress of direct water deficit and greater production of allelopathic substances in purple nutsedge under these conditions.

V. Nutrients

Plants may compete for nutrients such as phosphorus, potassium, nitrogen, calcium, magnesium, etc. (Black, 1973). Aldrich (1987) suggested that competition for phosphorus and potassium may occur at a later stage in the crop life cycle and may play a small part in crop yield reduction. However, competition for nitrogen may occur during earlier stages in the life cycle of a plant and result in a significant loss of crop yield. The nitrogen cycle is important as a limiting factor for primary production in many systems (Vitousek & Howarth, 1991). While nutrient stress may lead directly to competitive interference, it may also influence the level of

allelopathic compounds in plants under nutrient stress. Weeds under nutrient stress may produce higher amounts of allelopathic compounds, resulting ultimately in allelopathy. Similarly, a crop under nutrient stress may accumulate higher concentrations of allelopathic compounds and its residue may have allelopathic effects on weeds.

Nutrient-limited conditions may enhance allelopathic effects (Lehman & Rice, 1972; Rice, 1984), but adverse allelopathic effects may be overcome by addition of fertilizers in some instances, (Fisher et al., 1978; Bhowmik & Doll, 1984; Einhellig, 1989). Chou (1983) reported that phytotoxicity of certain organic acids can be overcome by ammonium ions. Allelopathic activity may be significant for certain species in nutrient limited soils (Klein & Blum, 1990). Dement and Mooney (1974) reported that cyanogenic glycoside accumulation in *Heteromeles arbutifolia* leaves was at its maximum levels during the warm, moist months of spring and summer, when nitrogen is most available. Freeman and Mossadeghi (1972) reported that the amount of glucosinolate sinalbin, *p*-hydroxybenzylglucosinolate in seeds of white mustard (*Sinapis alba*) increases more than 18-fold as the sulfur content increases from 0 to 3 milliequivalent/liter in the nutrient medium. Nitrogen deficiency, however, either increases glucosinolate concentration in plants or has no effect (Gershenzon, 1984). In most of the plant species studied, enhanced nitrogen supply leads to increased levels of alkaloids (Gershenzon, 1984). However, deficiency of potassium and phosphorus causes an increase in levels of soluble nitrogen compounds which may provide substrate for alkaloid biosynthesis (Stewart & Lahrer, 1980). Under phosphorus-deficient conditions the concentration of chlorogenic acid isomers increases (Koeppe et al., 1976). Higher amounts of phenolics leach from shoots and roots compared to phosphorus-sufficient plants. Hall et al. (1982) found that total phenolic content of *Helianthus annuus* increased with increased nutrient stress, and thus had significant inhibitory effects on seed germination of *Amaranthus retroflexus*. Stowe and Osborn (1980) found that phenolic allelochemicals were more inhibitory at low nutrient concentrations. However, pangola-grass (*Digitaria decumbens*) exhibited a strong competitive interference and became dominant under sufficient supply of nitrogen fertilizers, because higher application of nitrogen fertilizers to pangola-grass soils led to increased production of allelopathic compounds (Chou, 1983, 1989a; Chou & Lee, 1988). Thus, higher allelopathic compounds reduced the growth of other inferior competitors such as *Panicum repens* and *Imperata cylindrica* (Chou, 1989b).

Mihaliak and Lincoln (1985) reported that limited plant nitrate availability could result in higher amounts of leaf mono- and sesquiterpenoids in *Heterotheca subaxillaris*. Rice et al. (1960) reported that a significant increase in the concentration of allelopathic compounds resulting from phosphorus-deficient conditions might be important in old-field succession.

In spite of the increase of allelopathic compounds in response to stress, it is not clear whether a corresponding increase can also occur in the environment. In general, stress conditions have been considered to promote root exudation (Curl & Truelove, 1986). In allelopathic interference, natural release of compounds from living plants or from plant residue is very important (Tang et al., 1995). Svenningsson et al. (1990) studied the effect of water stress on the release of amino acids, lipids, and low–molecular weight carbohydrates from the roots of rape (*Brassica napus*) seedlings. They found a significant increase of sterols (β-sitosterol and campesterol) in natural release from water-stressed rape. However, amino acid concentrations were reduced in natural exudates. Kohl (1993) found that water stress enhanced the concentration of allelopathic compounds in the tuber and rhizosphere of purple nutsedge. There are gaps in our knowledge on how the altered levels of various secondary metabolites influence allelopathic potential of a plant species. More investigations need to be aimed at

studying this aspect under field conditions, and concentration of altered secondary metabolites should be observed in the rhizosphere.

Allelopathic compounds also influence accumulation of soil nutrients. The adverse effects of allelopathic chemicals on physiological, ecological, and chemical aspects of target plants have been studied, but it would be of interest to study the effects of allelopathic chemicals on soil chemistry as well (Inderjit & Dakshini, 1995). Allelopathic chemicals such as phenolics are known to influence nutrient cycling in aquatic and terrestrial ecosystems (Schlesinger, 1991; Appel, 1993; Inderjit & Mallik, 1997). Phenolics may affect phosphate availability by competing for anion absorption sites. They can bind to Al, Fe, and Mn, thus releasing phosphate otherwise bound to these cations (Appel, 1993; Kafkafi et al., 1988; Tan & Binger, 1986). Mn(IV) oxides are important in abiotic formation of organic nitrogen complexes in natural environments (Shindo & Huang, 1984; Wang & Huang, 1989). Soil nutrient retention problems in agroecosystems could be partly solved by using phenolic-containing mulch crops that are known to release nutrients (Fox et al., 1990; Palm & Sanchez, 1991). Monoterpenes have potential to alter rates of nutrient cycling, particularly of nitrogen and carbon (White, 1994). Bremmer and McCarty (1988) added monoterpenes at different levels, ranging from 10 to 500 μg g, to soils, and found that the level of inorganic nitrogen decreased significantly. Monoterpenes may alter N inputs to an environment by either stimulating or inhibiting N fixation (White, 1994). Monoterpenes react in the environment to enhance the conversion of oxides of nitrogen and sulphur to NO_3 and SO_4, respectively, which increase dry deposition of these compounds on the plant surface (White, 1994). Rice (1984) concluded that phenolic compounds such as caffeic and ferulic acids, myricetin, tannins, and tannin-derivative compounds inhibit oxidation of NH_4^+ to NO_2^- by *Nitrosomonas*. White (1986, 1994) reported the validity of his hypothesis that terpenoids may play an important role in inhibition of nitrification. McCarty and Bremner (1986) disagreed with the hypothesis that terpenoids or phenolic compounds can inhibit nitrification, and reported that terpenoids enhanced immobilization of ammonium N by soil organisms rather than inhibition of nitrification. A significant decrease in levels of terpenoids with N, P, and K fertilizations was reported (Gershenzon & Croteau, 1991). Bryant et al. (1983) suggested that addition of N fertilization may lower the production of C-based secondary metabolites. Northup et al. (1995) reported that *Pinus muricata*, through production of leaf litter rich in polyphenols, significantly influenced the release of dissolved organic nitrogen in soils. The observations that plants on nutrient-poor soils often have high amounts of phenols could be explained by these results (Chapin, 1995). The fact that many of the phenolics, terpenoids, and other C ring-based plant biochemicals can depress rates of decomposition and N mineralization, thus affecting soil N availability, indicates a need for a reassessment of many purported allelopathic compounds. Rice (1984) identified this effect on soil microbes allelopathy. Many ecologists studying decomposition and nutrient cycling, however, do not consider this to be allelopathy, because it can be explained by resource use and growth strategy of plants together with the energetics and nutritional requirement of bacterial and fungal components. The overwhelming evidence indicates that plant phenolics do play a significant role in allelopathic interactions (Inderjit, 1996). Phenolics, however, are the primary constituents of lignin, which is a critical component of leaf and stem structure, especially in slow-growing species. Furthermore, there is growing evidence that many of these compounds play a role in protection of leaves from UV-B radiation. It is important to demonstrate that phenolics, released by the plant, should have enough bioactive concentration and persistence in the rhizosphere in order to argue their probable involvement in allelopathy.

VI. Conclusion

On the issue of demonstrating allelopathy in natural systems, there are intense and potentially fruitful conflicts between contesting views. Unfortunately, many studies on chemical interference (allelopathy) were carried out in controlled environments and misinterpreted the phenomenon of allelopathy (see Putnam & Weston, 1986; Inderjit & Dakshini, 1995). Many studies attempted to separate these two mechanisms of interference (Nilsson, 1993). We, however, are of the view that resource competition and allelopathy may interact in natural systems. Williamson (1990) suggested that allelopathy in the scrub and sand hill vegetation in Florida may have evolved in order to reduce fire risk. There is convincing evidence that allelopathy has evolved as a result of resource competition and other ecological factors, and separation of resource competition and allelopathy might not be of much ecological relevance under natural systems. Rice (1984) discussed the significance of synergistic effects of stress factors, because these operate in combinations in natural systems. All these factors in combination may enhance competitive and/or allelopathic interference in a natural environment. In nature, both resource competition and allelopathic interactions may operate simultaneously. In addition, there are many co-linearities (e.g., concentration of allelopathic compounds is correlated with soil pH, soil moisture, soil organic matter, soil nutrients, etc.) that make it difficult to isolate a single factor. It is difficult or impossible to sort these things out. We may isolate co-linearities in controlled experiments, but in the process we create an environment that does not occur in nature. Ultimately, information on the mechanisms of interference (resource competition and allelopathy) is required, if we hope to develop a logical scenario to explain interference as it occurs in nature. While studying mechanisms of plant interference, both competition and allelopathy should be investigated. It is important to do a critical reassessment of possible causes of allelopathy given the soil microbial ecology, particularly the effects of secondary compounds on nutrient availability. Two-way tests should be run regardless of whether one is studying allelopathy or resource competition (Muller, 1965). The chance of resource–chemical interference in natural systems is higher than the chance of either resource or allelopathic interference alone. There is a pressing need to investigate resource-competition and allelopathy interactions in well-replicated field studies. Ecologists would value such studies under field conditions, which will add insights to the understanding of mechanisms of plant interference.

VII. Literature Cited

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